

Appendix A.9

Habitat Connectivity for Western Rattlesnake (*Crotalus oreganus*) in the Columbia Plateau Ecoregion

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Introduction

This species account describes the ecology, threats, and previous studies of Western rattlesnakes (*Crotalus oreganus*), and then uses this information to model connectivity of rattlesnakes across the Columbia Plateau Ecoregion. A previous modeling effort, the *Washington Connected Landscapes Project: Statewide Analysis* (WHCWG 2010), addressed several focal species across the entire state of Washington. Rattlesnakes were not included in this statewide effort, but were chosen as a focal species for the current ecoregional modeling across the Columbia Plateau. The Western rattlesnake is a species strongly associated with the shrubsteppe ecosystem that characterizes the Columbia Plateau. The species' potential distribution spans the majority of the Columbia Plateau Ecoregion, yet the movement ecology of rattlesnakes leaves them susceptible to fragmentation. Therefore, linkage modeling can be extremely useful for conservation planning of rattlesnakes, which may also represent other Columbia Plateau reptiles.



Western rattlesnake, photo by James Rosindell

Justification for Selection

The Western rattlesnake was chosen to represent cliff, canyon, and talus habitats. It is the only focal species that represents these habitats. These types of habitat are critical to the rattlesnake as they provide overwintering areas that all individuals require (Ernst & Ernst 2003). These types are also used as basking habitat and rookery sites for giving birth. However, aside from specific overwintering requirements, Western rattlesnakes are considered a habitat generalist and can be found in all natural vegetation classes.

Western rattlesnakes are affected by several threats across the Columbia Plateau Ecoregion. Although rattlesnakes can be considered a habitat generalist, the alteration of natural vegetation can have harmful consequences. Rattlesnakes are ambush foragers and require vegetation for cover. Furthermore, rattlesnake movements away from hibernacula are closely associated with areas of abundant prey. Alteration of habitat that reduces availability of small mammal species will indirectly harm snakes. Development is likely a complete barrier to rattlesnakes. Rattlesnakes do not persist around buildings both due to loss of habitat and food and direct human persecution. Traffic on roads kills many rattlesnakes (Jochimsen 2006; Andrews et al.

2008) and roads may additionally serve as conduits for spread of invasive grasses that further degrade habitat (Jochimsen 2006). Rattlesnakes are one of the most persecuted native vertebrate species, making people a major threat. People often swerve to hit rattlesnakes on roads and will often kill them whenever encountered. However, the most damaging form of persecution is searching and killing of animals at denning habitat and destruction of the dens themselves. Rattlesnakes communally den (sometimes by the hundreds) and so in the spring and fall, the opportunity exists for mass killing, which has happened. Fire is also likely a threat that influences rattlesnake populations through direct mortality as the fire is burning, as well as the trophic effects of altered habitat. Jenkins and Peterson (2008) found that radio-tracked rattlesnakes used burned areas as foraging grounds. However, these areas had lower small mammal biomass and the snakes therefore had a lower body mass, which would probably translate to decreased fitness. Currently, it is unclear the threat that wind turbines or transmission lines pose, although both likely disturb habitat and are accompanied by a road infrastructure that adversely affects snake populations.

The Western rattlesnake was scored as Excellent for other selection criteria (See Appendix E). Rattlesnakes are one of the best studied snakes in general, and there is a large database of observations across Washington. Therefore, there is enough information to develop a rigorous model. It has a movement scale that is relevant to the Columbia Plateau ecoregional scale. Individuals can move up to several kilometers at a time (Jørgensen et al. 2008), but individuals are very unlikely to move out of the general Columbia Plateau region. The dispersal and migration of rattlesnakes are tightly tied to several landscape features, so changes to the landscape will limit their dispersal. Furthermore, roads can be barriers interrupting important migratory paths from dens to feeding ranges. Finally, the communal denning aspect of rattlesnake life history makes monitoring their populations feasible (Parker & Brown 1973; Diller & Wallace 2002; Jenkins et al. 2009). Rattlesnakes are also an excellent species for radio-tracking to determine how landscape variables influence snake movement (Jørgensen et al. 2008).

Rattlesnakes are an especially appropriate species to include for Columbia Plateau modeling as they occur in all of the natural habitats found in the ecoregion and are one of the most identifiable species associated with the Columbia Plateau Ecoregion. They are the only focal species that requires rock outcrops as critical habitat (for dens), and shrubsteppe vegetation is additionally critical for feeding activities. Thus, a habitat network for Western rattlesnakes would identify connected natural habitats across the Columbia Plateau, and therefore serve to represent the needs of many species in the region.

The Western rattlesnake is not federally listed, and its rank both globally and statewide is 5 (NatureServe 2011), indicating secure populations. It is listed as threatened in British Columbia (COSEWIC 2004) due to its restricted distribution in the province.

Distribution

The Western rattlesnake is one of the most widespread reptiles in North America, with presence in British Columbia, Washington, Oregon, California, Idaho, Nevada, Arizona, Utah, Colorado, Wyoming, and Mexico. However, the species is divided into several subspecies, with only one subspecies occurring in Washington, the Northern Pacific rattlesnake (*C. o. oregonus*). In

addition to Washington, it is the only subspecies in British Columbia, and it also occurs in parts of Idaho, Oregon, and California. There are no known range-wide contractions of the subspecies, although finer scale declines have likely occurred due to human interference with denning habitat and direct killing of snakes.

The broad-scale limiting factors for rattlesnake distributions are likely related to climatic factors that tend to be associated with elevation and precipitation. The boundaries for the distribution of the Northern Pacific rattlesnake are largely constrained by mountain ranges and wet coastal conditions. Therefore, dry and warm climates are essential for this rattlesnake to be found. Its northern extent in British Columbia is likely limited by temperature, and it is replaced in the southern extent of its range by another subspecies, the Southern Pacific rattlesnake (*C. o. helleri*). At a finer scale, rattlesnakes are limited by the presence of areas with suitable denning habitat. Optimal dens are found on rocky slopes that are south-facing to provide the warmest temperatures for basking and overwintering. Therefore, any rattlesnake occurrence is necessarily within a few kilometers of appropriate denning habitat. In the summer, the limiting factor is the presence of small mammal prey. In the Columbia Plateau region, rattlesnakes could potentially be found across the entire region, as the channeled scablands and land forms created by other geologic processes contain extensive suitable denning habitat.

Because rattlesnakes typically return to the same den each year and are concentrated in these areas, the potential for isolation is high if the surrounding landscape is cleared or fragmented by roads. To my knowledge, there is only one fine-scale genetic study on Northern Pacific rattlesnakes in Washington (J. Dobry, unpublished data). This study found different mitochondrial haplotypes at den sites only several kilometers apart on the same side of the Snake River near Pullman, Washington. This suggests some degree of genetic isolation, in an area that was heavily impacted by the creation of Granite Lake reservoir, which may have had a role in this isolation, and would not be as applicable across the entire plateau. In another subspecies of the Western rattlesnake, the Great Basin rattlesnake (*C. o. lutosus*), there was little genetic subdivision across the study area (largely protected as part of a Department of Energy installation), suggesting high natural gene flow among dens (Parsons 2009). In a dwarfed Western rattlesnake subspecies, the midget faded rattlesnake (*C. o. concolor*), gene flow was much more restricted and roads were significantly correlated with reduced gene flow across southern Wyoming (Spear et al. 2011). Thus, we expect that the natural population structure of this species expresses high connectivity, but human activities that fragment the landscape have potential to isolate populations.

We are not aware of any translocations or reintroductions across the study area. It is not a species that has required reintroductions for conservation purposes, and is an unlikely candidate for purposeful translocations. The one potential exception to this is short distance translocations of “nuisance snakes” that people want removed from their land. However, such translocations in other areas usually result in the snake returning to the initial spot and are ultimately unsuccessful. Therefore, any population of rattlesnakes in Washington is almost certainly the result of natural processes.

Habitat Associations

Active Season Habitat

Rattlesnakes can be found in a variety of habitats during the active season, including shrub, grassland, forest, cliffs/talus, and riparian. Our knowledge of habitat use by rattlesnakes has largely been shaped by radio-telemetry and trapping studies. While there are not published studies of rattlesnake habitat use in Washington, several studies have taken place using Western rattlesnakes in various other locations. At the northern extent of the range of Northern Pacific rattlesnakes in British Columbia, Gomez (2007) found that snakes surprisingly spend more time in Douglas-fir (*Pseudotsuga menziesii*) forest relative to availability. However, the only other habitats available were bunchgrass and ponderosa pine (*Pinus ponderosa*), with dens located in the bunchgrass habitat. Therefore, the use of forested habitat may be related to the lack of shrub or cliff habitat. In southern Idaho, Great Basin rattlesnakes used undisturbed shrub and burned shrub much more frequently than grazed habitat (Jenkins & Peterson 2008). However, snakes that used burned areas as their core range had lower mass than those in undisturbed habitat, suggesting this was not optimal habitat. A trapping and hand-capture study in another location in southern Idaho found snakes most frequently in canyon rims and rock outcrops, with big sagebrush (*Artemisia tridentata*) being the vegetation most often associated with snakes (Diller & Wallace 1996). Agriculture and sand had the lowest captures of rattlesnakes. Finally, Grand Canyon rattlesnakes (*C. o. abyssus*) used riparian areas (within 10 m of water) and talus preferentially relative to its availability, while snakes seemed to avoid floodplain habitat (greater than 10 m from water; Reed & Douglas 2002).

Overwintering Habitat

Overwintering habitat for rattlesnakes is characterized primarily by rocky areas on slopes (Parker 2003; Cooper-Doering 2005; Gomez 2007; Clark et al. 2008). Aspect, geology, and climate are also important for Western rattlesnake hibernacula, although the relative importance of these factors can be different depending on subspecies and study area. To our knowledge, there have been three studies that have investigated factors important to Western rattlesnake hibernacula. Cooper-Doering (2005) used a Boolean model to identify denning habitat for Great Basin rattlesnakes on the Snake River plain of southeastern Idaho. She identified three variables that predicted denning habitat: slope between 30 and 80%, aspect between 90 and 260 degrees, and Pleistocene lava flows. In Nevada and Utah, Hamilton and Nowak (2009) found that insolation values of Great Basin rattlesnake dens were higher than other available areas. Finally, Spear et al. (2011) used a validated maximum entropy model (Maxent) to predict den areas for midget faded rattlesnakes in Wyoming and found two variables were included in the model, distance to rock outcrop and annual temperature range. Given the success of the Maxent modeling method after field validation in the midget faded rattlesnake study, we decided to use maximum entropy modeling to identify Western rattlesnake habitat in the Columbia Plateau Ecoregion.

Sensitivity to Roads and Traffic

Western rattlesnakes have high sensitivity to traffic primarily due to road mortality and avoidance of road habitats. Several studies have documented high occurrence and mortality of Western rattlesnakes on roads. Klauber (1939) drove extensively in the San Diego area and found 69 dead Southern Pacific rattlesnakes. Sullivan (2000) drove a road in California on repeated surveys in the late 1970s and late '90s, and discovered a total of 292 Northern Pacific

rattlesnakes on the road. Jochimsen (2006) drove a standardized route in southeastern Idaho over two years and observed 72 Great Basin rattlesnakes. Finally, models of gene flow in midget faded rattlesnakes included roads as an important variable constraining gene flow, and there was a reduction in adult males, the age class most likely to be impacted by roads (Spear et al. 2011). Finally, Jenkins (2007) radio-tracked Great Basin rattlesnakes in southeastern Idaho and found many snakes limited their movement at road edges and did not cross roads. Therefore, rattlesnakes appear to be highly susceptible to road mortality, and even if snakes are not killed on roads, they may avoid roads to some extent which would also decrease connectivity.

Sensitivity to Development

Western rattlesnakes likely have high sensitivity to development, both as a result of habitat destruction and direct persecution. Fitch (1949) documented 819 Northern Pacific rattlesnakes killed near buildings over five years around the author's study site; he considered this an underestimate as these were snake mortalities that were reported directly to him. Furthermore, I know of no viable rattlesnake populations that have been reported within a developed area (although populations will be found near developed areas in appropriate habitat).

Sensitivity to Energy Development

Energy development likely has a detrimental impact on Western rattlesnakes, although the response of individuals or populations to energy development has not been directly studied. The strongest impact of energy development is likely to be the resulting road infrastructure surrounding development which will lead to increased mortality of snakes. However, the relative risk of mortality of energy roads compared to other road types is unknown. Energy development also brings humans into contact with rattlesnakes, and energy workers likely will at least occasionally kill rattlesnakes (T. Warfel, personal communication). Finally, any oil and gas drilling or wind turbines that are located directly on den habitat could lead to the destruction of the den and the resulting mortality of individuals using that den site.

Sensitivity to Climate Change

Little direct data is available, but there is potential for climate change to influence Western rattlesnake populations. As ectotherms, rattlesnakes are highly influenced by temperature. For instance, a habitat model of midget faded rattlesnake den sites identified annual temperature range as one of the key variables (Spear et al. 2011). There was only a limited set of temperature range values that was suitable for dens, indicating that climate change could shift the locations of suitable den habitat, at least for this rattlesnake population. Furthermore, active season habitat in Western rattlesnakes is largely driven by prey availability (Jenkins & Peterson 2008), so any effect of climate change on prey species will affect rattlesnakes as well.

Dispersal

Most significant movements of Western rattlesnakes occur during seasonal movements from hibernacula to core activity ranges in the summer and back to the hibernacula in the fall. There is relatively limited movement around the hibernacula, but there can be a number of short-distance movements on the core activity ranges. There have been several radio-telemetry studies that have examined movements in different subspecies of Western rattlesnakes and the closely related prairie rattlesnake (*C. viridis*; Table A.9.1). There has been quite a range of movement distances

from dens to activity ranges, but in general distances have ranged from 1 to 4 km, with males generally moving further than females (Table A.9.1). To my knowledge, there has not been a published study of rattlesnake movement distances for the Columbia Plateau, but Gomez (2007) studied the same subspecies (Northern Pacific rattlesnake) in British Columbia and found maximum distances of 3.5 km at one den and 1 km at another nearby den. Mean distances were not reported in this study. The two dens were surrounded by a different habitat matrix, and thus movement distances of rattlesnakes are likely not independent of habitat quality (probably directly due to prey availability; Jørgensen et al. 2008). Other subspecies of Western rattlesnake had mean distances less than 1.5 km. I also examined movement distances for prairie rattlesnakes, as prairie and Western rattlesnakes were once considered a single species. In most cases prairie rattlesnakes had only slightly higher distances moved from the dens, ranging from 1 to 5 km, with the notable exception of one study in Alberta in which rattlesnakes moved 15–20 km from the den (Table A.9.1). These studies collectively support a pattern of greater movement distances to activity ranges with latitude, although there is still considerable variation within some areas (Jørgensen et al. 2008). Therefore, we can likely assume that rattlesnakes in the Columbia Plateau would move around 2–3 km from hibernacula (greater than southern Idaho, less than British Columbia).

Table A.9.1. Movement and home range sizes for different subspecies of Western rattlesnake (*Crotalus oregonus*) as well as the closely related prairie rattlesnake (*C. viridis*).

<i>Subspecies (sex)</i>	<i>Location</i>	<i>Distance from den (km)</i>		<i>Home range size (ha)</i>		<i>Citation</i>
		<i>mean</i>	<i>maximum</i>	<i>core</i>	<i>total</i>	
<i>C. oregonus oregonus</i>	BC Site 1		3.568			Gomez 2007
<i>C. oregonus oregonus</i>	BC Site 2		~ 1			Gomez 2007
<i>C. oregonus lutosus</i>	ID	1.47		22.7		Jenkins 2007
<i>C. oregonus concolor</i> (males)	WY	0.779		56.6	301.2	Parker & Anderson 2007
<i>C. oregonus concolor</i> (females)	WY	0.681		27.6	196	Parker & Anderson 2007
<i>C. oregonus concolor</i> (gravid females)	WY	0.115		2.5	12	Parker & Anderson 2007
<i>C. viridis</i>	ID	1.32		21.1	96.3	Bauder 2010
<i>C. viridis</i>	WY	5.13				Duvall et al. 1985
<i>C. viridis</i> (males)	WY	2.57				King & Duvall 1990
<i>C. viridis</i> (females)	WY	2.03				King & Duvall 1990
<i>C. viridis</i> (males)	AB	15.1				Didiuk 1999
<i>C. viridis</i> (females)	AB	20				Didiuk 1999
<i>C. viridis</i> (females)	AB	2.76				Jorgensen et al. 2008

Home-range sizes can be calculated for rattlesnakes in two different ways. Home range could be based on all movements, which would combine migration from den to activity area as well as activity movements. A second approach would be to calculate home range as only within the core activity area after migration from the den has already occurred. Both measures have some utility for connectivity modeling, as the first measure of home range gives the upper range for area that an individual could move through. However, as much of the movement from den to activity areas are straight-line and directed, home range based only on core activity areas presents a more realistic area occupied from the aspect of mating and foraging. Fewer radio-

telemetry studies have estimated home range sizes, but those that have suggest an average of 25–50 ha for core home ranges and 100–300 ha for total movement home range (Table A.9.1). The one exception is gravid females, a group that have very low movements and home range (Parker & Anderson 2007).

Conceptual Basis for Columbia Plateau Model Development

Overview

Western rattlesnake habitat use is well characterized for overwintering denning areas, but less so for summer habitat use away from the den. This is largely because rattlesnakes communally overwinter, and so dens are very conspicuous during spring emergence. In contrast, snakes are largely solitary (except for mating activities) during the summer season and are much more difficult to study, requiring radio-telemetry studies or very widespread trapping studies. Rattlesnake dens are primarily characterized by rocky slopes on southern and eastern aspects, often along river valleys (Ernst & Ernst 2003). Western rattlesnakes have a broad species range, and therefore the specific variables associated with movement do vary across studies. For instance, Western rattlesnakes in British Columbia preferentially moved in conifer forests (Gomez 2007), a habitat type missing from much of the Columbia Plateau. However, consistencies among studies include associations with native vegetation (generally shrub or forest), riparian areas, and talus areas (Diller & Wallace 1996; Reed & Douglas 2002; Gomez 2007; Jenkins & Peterson 2008; Bauder 2010).

Most rattlesnake studies have occurred in landscapes with relatively low human development. In large part, this is likely due to the lack of existing populations in human-dominated areas. However, this does make it difficult to understand how anthropogenic infrastructure influence snake movement. Certainly snakes are very susceptible to road mortality (Jochimsen et al. 2004) and some genetic studies have demonstrated that roads reduce connectivity (Clark et al. 2010; Spear et al. 2011). There currently are concerns with how wind development might influence snake populations, but data is lacking.

Therefore, our main source for assigning resistance to land cover elements was largely past field studies, whereas anthropogenic variables were largely assigned through expert opinion due to the lack of field studies. Nevertheless, we considered roads and development as likely the largest impediments to movement and connectivity, and native vegetation or rocky areas in lower elevations as the least resistant landscapes.

Movement Distance

Most movement distances by Western rattlesnakes are only a few kilometers, and thus most connectivity occurs between close populations (Table A.9.1). However, rare long-distance movements are much more difficult to detect and at least one study did demonstrate that rattlesnakes are capable of much longer movements. The closely related prairie rattlesnake moved up to 20 km away from the denning area in Alberta, with a total movement distance of 44 km including the return trip to the denning area (Didiuk 1999). I chose a cost-weighted distance (CWD) of 50 km to account for the potential long-distance movement ability, even if it rarely occurs. Furthermore, there will undoubtedly be actual den locations not included in our HCA

models, and thus a larger cost-weighted distance should help to ensure that actual connectivity corridors are not eliminated.

Habitat Concentration Areas

To model habitat suitability for habitat concentration areas (HCAs), I used an empirically driven approach using Maxent species distribution modeling as opposed to parameterization of habitat suitability values. I used this approach because we had available a large number ($n = 400$) of known occurrence points for Western rattlesnakes in Washington. Therefore, instead of using expert opinion to determine habitat suitability scores, I correlated the known occurrences with the environmental layers to produce a map of habitat suitability (and as a side benefit identify the most important variables). Maxent has been demonstrated to be an accurate modeling method (Elith et al. 2006), and was successfully used to model hibernacula habitat in the Western rattlesnake subspecies *C. o. concolor* (Spear et al. 2011). However, Maxent does require careful input of observations and designation of pseudoabsence points (points that represent the available habitat) to compare with presence points. In particular, sampling bias in observations can lead to a model that assigns high habitat suitability to areas that were simply sampled often. The database of observations were largely from the Washington Department of Fish and Wildlife database managed by Lori Salzer, but also included observations provided by Jason Dobry (Amplicon Express) and John Rohrer (USFS). There was not a standardized protocol to collect all these observations, and there was likely a bias of observations along roads and on public lands. To attempt to address some this bias, we spatially filtered all observations so that there would be one observation within a radius of 1 km. This reduced the number of data points to 227 (Fig. A.9.1). Maxent is a presence-only modeling method, which means that it requires input of pseudoabsence points that represent the available habitat to compare with actual observations. However, placing pseudoabsence points outside of the area of sampling could also bias models (VanDerWal et al. 2009; Lobo et al. 2010). Therefore we selected 10,000 pseudoabsence points constrained within a minimum convex polygon of all observation points.

Another difference with implementing Maxent rather than the habitat suitability parameterization used by other focal species leads is that Maxent requires continuous environmental variables instead of categorical variables. For the topographic and soil variables, this was straight-forward as the raw GIS base layers are continuous. Specifically, I included compound topographic index, elevation, solar insolation, slope, soil depth, soil available water capacity, and vector ruggedness. However, the land cover, housing density, and anthropogenic feature layers are categorical by nature, and therefore I needed to convert the layer to a continuous variable. For land cover, instead of trying to represent each land cover category, I only considered rock outcrops for the habitat model. This is because the observations are undoubtedly biased toward den locations, and den locations should be overwhelmingly driven by presence of rock and talus. I calculated the distance of each grid cell from the nearest rock outcrop category and used that as the environmental layer. I also used the distance to rock outcrops as predicted by the landform layer to provide an alternative rock outcrop layer in case it had a better correlation than the land cover categories. Finally, I calculated distance to housing density less than 80 ac per housing unit.

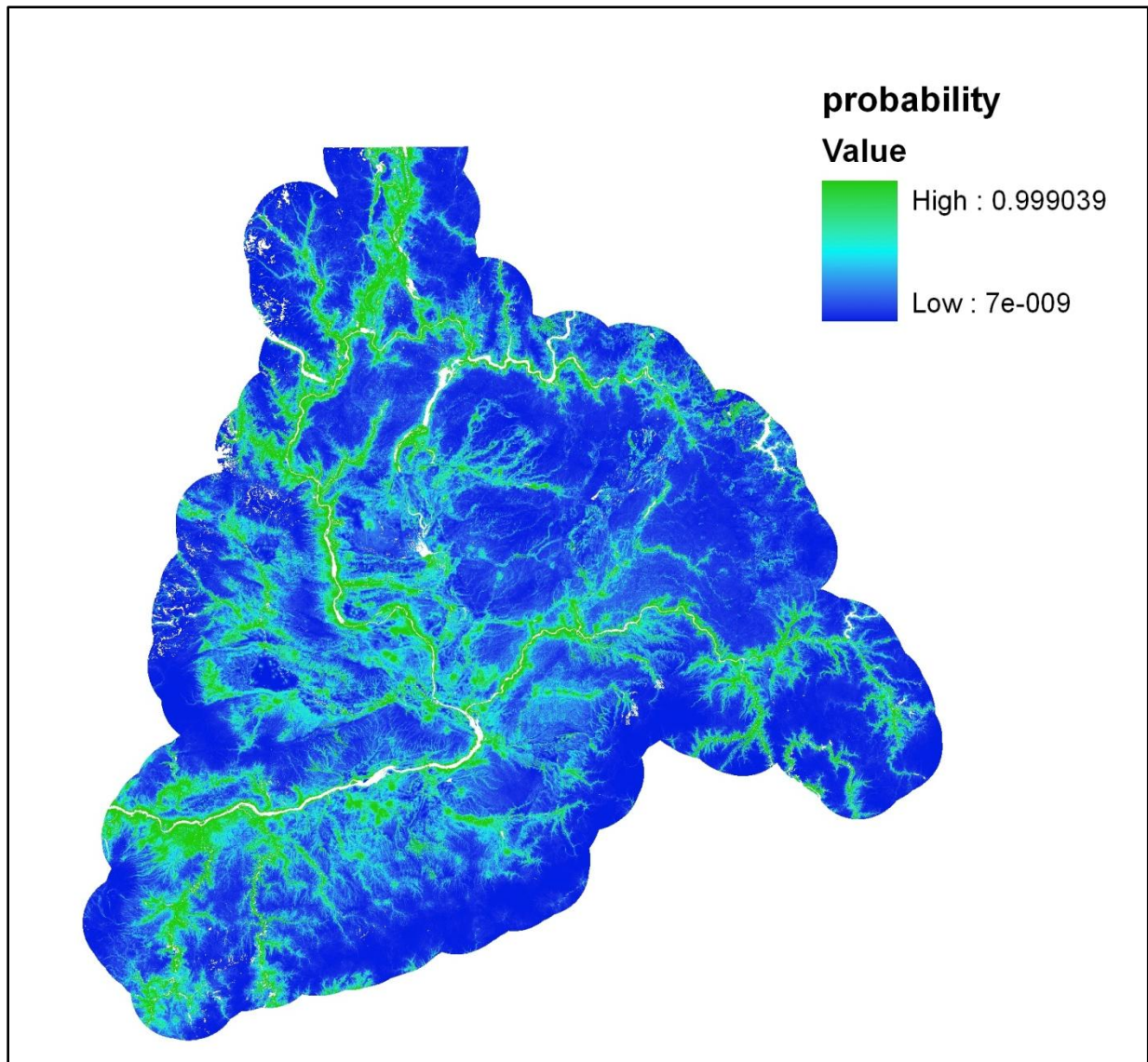


Figure A.9.1. Output map of Maxent results (legend of probability values in upper right). White squares represent the observed locations of Western rattlesnakes used to create the model.

Two variables had the strongest contribution for predicting rattlesnake presence—distance to rock land cover and elevation (Table A.9.2). In both cases, there was a negative relationship; that is, areas near rock outcrops and at low elevations were most important for predicting rattlesnake presence (Fig. A.9.2a, b). The second tier of contributing variables was solar insolation and the soil water capacity. Interestingly, probability of rattlesnake occurrence was greatest at the lower values of solar insolation, with a secondary spike at intermediate levels of solar insolation and a sharp drop at the highest values of solar insolation (Fig. A.9.2c). This is surprising as rattlesnakes are expected to require greater solar insolation, and a study of rattlesnake hibernacula in central Washington found all studied dens to have south aspects (greater insolation), but were found at shallower slopes than at random (Gienger & Beck 2011). The shallower slopes would reduce the solar insolation, and therefore the bump seen in Figure A.9.2c between values 3000–3500 may represent the shallow south-facing slopes that are used as

denning habitat. Furthermore, although many of the observations are at or near den sites, many of the observations are not at denning areas and snakes may move frequently through low insolation areas. In fact, in the summer, it may be common for snakes to avoid the areas of highest solar insolation. This would be problematic if we were attempting to model only den habitat, but HCAs should represent both winter and summer habitat for the snakes. The reliance of rock outcrop should allow representation of good overwintering habitat in the HCAs, and the relationship with lower solar insolation might pick up areas used during the summer that would not be included if we were only modeling den habitat. Finally, as might be expected, drier soils were correlated with rattlesnake occurrence (Fig. A.9.2d).

Table A.9.2. Percent contribution of each variable to the Maxent Western rattlesnake habitat model.

<i>Variable</i>	<i>Percent Contribution</i>
Distance to rock (landcover)	29.7
Elevation	26.1
Solar insolation	15.1
Soil available water capacity	11.3
Soil depth	7.4
Vector ruggedness	4.5
Distance to housing	3.1
Distance to outcrop (landform)	1.5
Slope	1
Compound topographic index	0.4

The output of the Maxent run is a continuous map of probability of rattlesnake occurrence. However, the probability values do not translate literally, and instead the output includes statistical thresholds that help determine what probability values should delimit likely habitat. These thresholds were used to determine the minimum average habitat value for habitat concentration areas (HCAs) and the minimum binary threshold. The value that has the greatest statistical support for delineating habitat is the maximum sensitivity plus specificity threshold. This statistic maximizes both the ability of the model to correctly identify actual habitat, but also the accuracy with which the model predicts unsuitable habitat when the habitat is actually unsuitable. This value was 0.3 for the rattlesnake model. For the minimum binary cutoff, I used a value of 0.07 which was the minimum probability value that included all observations. I did make one adjustment to the Maxent habitat surface before running the HCA model. This was to change the probability value of all roads and railroads to zero. I did not include roads in the Maxent model because of the bias of observations towards roads, but clearly the linear road and railroad surfaces are not suitable rattlesnake habitat. I chose 2.5 km as the home range radius, as this seemed to be a justified average distance moved from the den based on the movement values in the literature. Finally, the minimum HCA size was 1250 ha as decided by the Columbia Plateau analysis team.

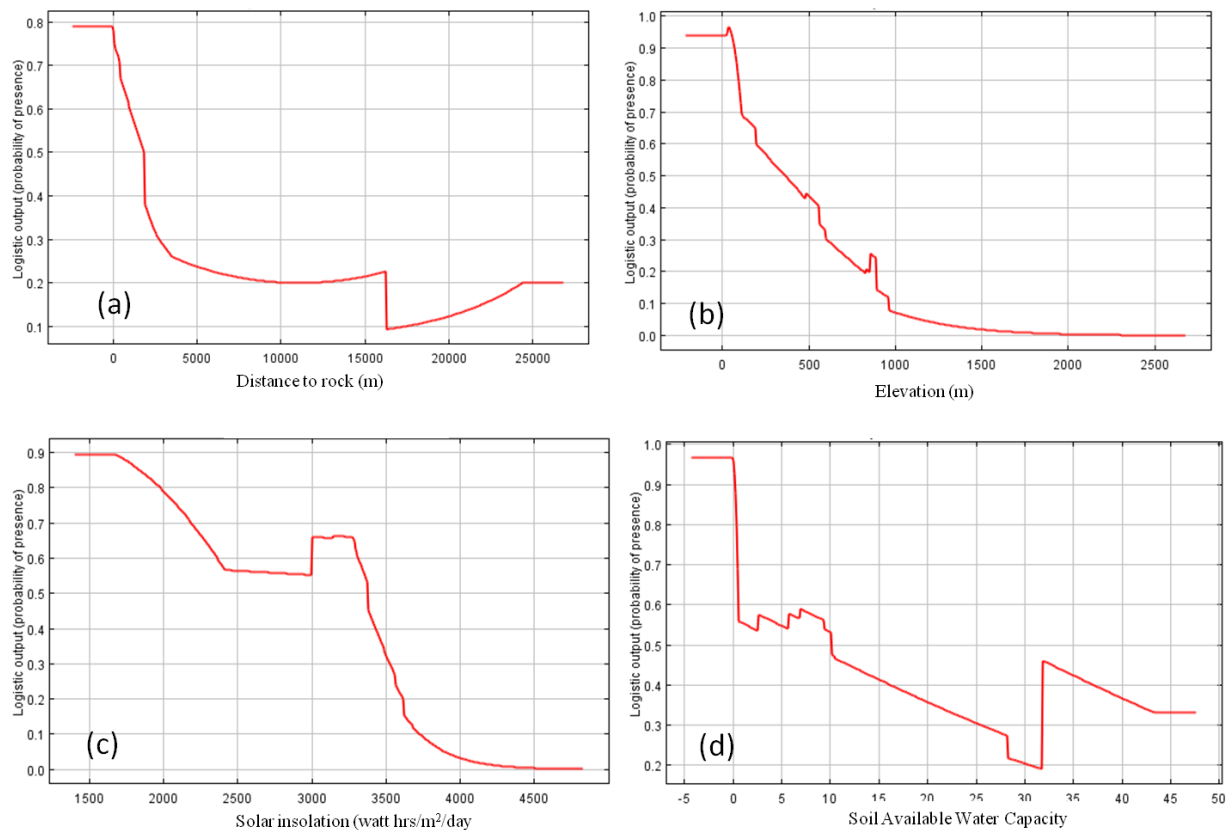


Figure A.9.2. Correlation of highest contributing environmental variables with predicted Western rattlesnake occurrence.

I initially ran the HCAs based on 30 m resolution, but later scaled the resolution up to 90 m for ease of downstream modeling. Initial evaluation of the HCA polygons were largely satisfactory, but one region (Methow Valley) was not included as an HCA despite known presence of dens. The reason for the lack of an HCA polygon was that this region is at the edge of the rattlesnake’s range and at higher elevation than most populations, and thus there was not a sufficient extent of predicted habitat to create an HCA of minimum size. To add an HCA in this region, I ran a Maxent model using only the spatial extent of the Methow Valley, and ran the HCA toolkit on this layer. We manually added this polygon to the overall HCA layer. Finally, there were three small HCAs in areas with known observations that were present in the 30 m HCA layer but were absent from the 90 m layer. As these polygons were in areas without other HCAs, I included them in the final HCA polygon layer so as to not artificially disrupt connectivity.

Resistance and Habitat Values for Landscape Features

I used the expert opinion method to determine resistance scores for the parameters included in the model (Table A.9.3). To the greatest extent possible, I used published studies to inform the relative ranking of resistances (these studies are referenced in the above sections). However, there were several categories for which empirical research did not exist, and therefore I used my and other’s expert knowledge from working on rattlesnake populations. The general approach I took for resistance parameterization was to create relative levels of resistance to assign for

categories. This ranged from 0 (no movement resistance other than Euclidean distance) to 1000 (equivalent 30 km cost-weighted distance to move through a grid cell) which I considered to be effectively a complete barrier to movement. The greatest tier of resistance ranged from 500 to 1000 (little to no movement) and was assigned to high density housing, interstate and major highways, wind turbine locations, and high elevations. The second tier ranged from 100 to 200 (difficult to move through, but not complete barrier) and was assigned to more minor roads, disturbed habitat, and intermediate housing densities. All of the categories assigned resistance of 100 or greater were either anthropogenic infrastructure or, in the case of high elevations, conditions outside the niche of the species in Washington. Thus, such high values of resistance largely represent the high direct mortality risk that these environments represent. The next tier, ranging from 20 to 50, was assigned to agriculture, invasive vegetation, railroads, lower housing density, or extremely rough terrain. These were landscape elements that I expected rattlesnakes to avoid or have difficulty moving through, but would not be movement barriers. Finally, resistance values of 1–10 represented environment types that rattlesnakes might commonly move through, with values closer to 10 representing types that would be somewhat resistant, but would not be expected to stop movement. These categories include most natural land-cover categories, as well as the topographical variables.

(continued on page A.9-15)

Table A.9.3. Landscape features and resistance values used to model habitat connectivity for Western rattlesnakes.

<i>Spatial data layers and included factors</i>	<i>Resistance value</i>	<i>Habitat value*</i>
Landcover/Landuse		
Grassland_Basin	0	n/a
Grassland_Mountain	2	n/a
Shrubsteppe	0	n/a
Dunes	2	n/a
Shrubland_Basin	0	n/a
Shrubland_Mountain	2	n/a
Scabland	2	n/a
Introduced upland vegetation_Annual grassland	50	n/a
Cliffs_Rocks_Barren	0	n/a
Meadow	5	n/a
Herbaceous wetland	5	n/a
Riparian	0	n/a
Introduced riparian and wetland vegetation	10	n/a
Water	10	n/a
Aspen	0	n/a
Woodland	0	n/a
Forest	2	n/a
Disturbed	100	n/a
Cultivated cropland from RegapNLCD	50	n/a
Pasture Hay from CDL	10	n/a
Non-irrigated cropland from CDL	10	n/a
Irrigated cropland from CDL	50	n/a
Highly structured agriculture from CDL	50	n/a
Irrigated/Not Irrigated/Cultivated Crop Ag Buffer 0 – 250m from native habitat	10	n/a
Irrigated/Not Irrigated/Cultivated Crop Ag Buffer 250 – 500m from native habitat	30	n/a
Pasture Hay Ag Buffer 0 – 250m from native habitat	2	n/a
Pasture Hay Ag Buffer 250 – 500m from native habitat	5	n/a
Elevation (meters)		
0 – 250m	0	n/a
250 – 500m	0	n/a
500 – 750m	0	n/a
750 – 1000m	0	n/a
1000 – 1250m	0	n/a
1250 – 1500m	10	n/a
1500 – 2000m	50	n/a
2000 – 2500m	500	n/a
2500 – 3300m	500	n/a
Slope (degrees)		
Gentle slope Less than or equal 20 deg	5	n/a
Moderate slope Greater than 20 less than equal to 40 deg	0	n/a
Steep slope Greater than 40 deg	5	n/a
Ruggedness		
Very gentle terrain (or surface water)	10	n/a
Gentle terrain	5	n/a
Moderate terrain	0	n/a
Rough terrain	5	n/a
Very rough terrain or escarpment	20	n/a
Compound Topo Index		
Dry zone	0	n/a
Potential dry to moist zone	0	n/a
Potential wet zone	5	n/a
Insolation		

<i>Spatial data layers and included factors</i>	<i>Resistance value</i>	<i>Habitat value*</i>
Very low insolation	10	n/a
Low insolation	5	n/a
Moderate insolation	2	n/a
High insolation	0	n/a
Very high insolation	0	n/a
Housing Density Census 2000		
Greater than 80 ac per dwelling unit	0	n/a
Greater than 40 and less than or equal 80 ac per dwelling unit	20	n/a
Greater than 20 and less than or equal 40 ac per dwelling unit	100	n/a
Greater than 10 and less than or equal 20 ac per dwelling unit	200	n/a
Less than or equal 10 ac per dwelling unit	1000	n/a
Roads		
Freeway Centerline	800	n/a
Freeway Inner buffer 0 – 500m	20	n/a
Freeway Outer buffer 500 – 1000m	4	n/a
Major Highway Centerline	600	n/a
Major Highway Inner buffer 0 – 500m	10	n/a
Major Highway Outer buffer 500 – 1000m	2	n/a
Secondary Highway Centerline	180	n/a
Secondary Highway Inner buffer 0 – 500m	4	n/a
Secondary Highway Outer buffer 500 – 1000m	0	n/a
Local Roads Centerline	45	n/a
Local Roads Inner buffer 0 – 500m	1	n/a
Local Roads Outer buffer 500 – 1000m	0	n/a
Railroads Active		
Railroads Active Centerline	45	n/a
Railroads Active Inner buffer 0 – 500m	1	n/a
Railroads Active Outer buffer 500 – 1000m	0	n/a
Railroads Inactive		
Railroads Inactive Centerline	5	n/a
Railroads Inactive Inner buffer 0 – 500m	1	n/a
Railroads Inactive Outer buffer 500 – 1000m	0	n/a
Transmission Lines		
Less Than 230KV One Line Centerline	5	n/a
Less Than 230KV One Line Inner buffer 0– 500m	1	n/a
Less Than 230KV One Line Outer buffer 500 – 1000m	0	n/a
Less Than 230KV Two or More Lines Centerline	10	n/a
Less Than 230KV Two or More Lines Inner buffer 0 – 500m	1	n/a
Less Than 230KV Two or More Lines Outer buffer 500 – 1000m	0	n/a
Greater Than or Equal 230KV One Line Centerline	5	n/a
Greater Than or Equal 230KV One Line Inner buffer 0 – 500m	1	n/a
Greater Than or Equal 230KV One Line Outer buffer 500 – 1000m	0	n/a
Greater Than or Equal 230KV Two Lines Centerline	10	n/a
Greater Than or Equal 230KV Two Lines Inner buffer 0 – 500m	1	n/a
Greater Than or Equal 230KV Two Lines Outer buffer 500 – 1000m	0	n/a
Wind Turbine		
Wind turbine point buffer 45m radius	500	n/a
Buffer zone beyond point buffer 0 – 500m	10	n/a
Buffer zone beyond point buffer 500 – 1000m	5	n/a
Irrigation Infrastructure		
Irrigation canals	5	n/a

*Habitat values were not used to model habitat concentration areas.

Modeling Results

Resistance Modeling

As expected, based on the resistance surface parameterization, movement potential for rattlesnakes is disrupted most by areas with roads and urban areas (Fig. A.9.3). The most apparent areas of high resistance are the linear features of interstate and major highways, and the urban centers of Spokane, Tri-Cities, Yakima, Ellensburg, and Wenatchee. There are a few areas in the western portion of the study area that appear to have large patches of low resistance; these are concurrent with large areas of restricted access such as the Hanford Site, Yakima Training Center, and Yakama Reservation. This is consistent with the pattern seen in areas such as southern Idaho, in which the restricted access Idaho National Laboratory has high density rattlesnake populations. However, the disadvantage of relying on large restricted-access areas for low resistant refuges is that activities that may occur on these ranges are not modeled in our analysis and could have the potential to increase resistance (i.e., military firing exercises). Also, in the case of the Columbia Plateau, these large areas are at the western border of the Western rattlesnake's range in Washington, and thus may not be as efficient for overall landscape connectivity.

In the core of the Columbia Plateau, the extent of agricultural land in Whitman, Garfield, and Adams counties leads to high resistance across much of the area. However, eastern Adams County has large portions of low resistance habitat, and much of the Swanson Lakes Wildlife Area and Upper Crab Creek of Lincoln County to the northwest has low resistance as well. However, the patches of good movement habitat in these two areas are separated by I-90. The northern region of the Columbia Plateau has generally low resistance, with the exception of high-elevation mountains and the agricultural areas of the Okanogan Valley. This suggests connectivity with British Columbia, although this was not explicitly modeled in our analysis.

One area of modeled low resistance that is not considered rattlesnake habitat is Benewah and Latah counties in central Idaho. This area is modeled as low resistance because of intact native habitat (in this case forest), but is actually not suitable for rattlesnakes due to climatic constraints.

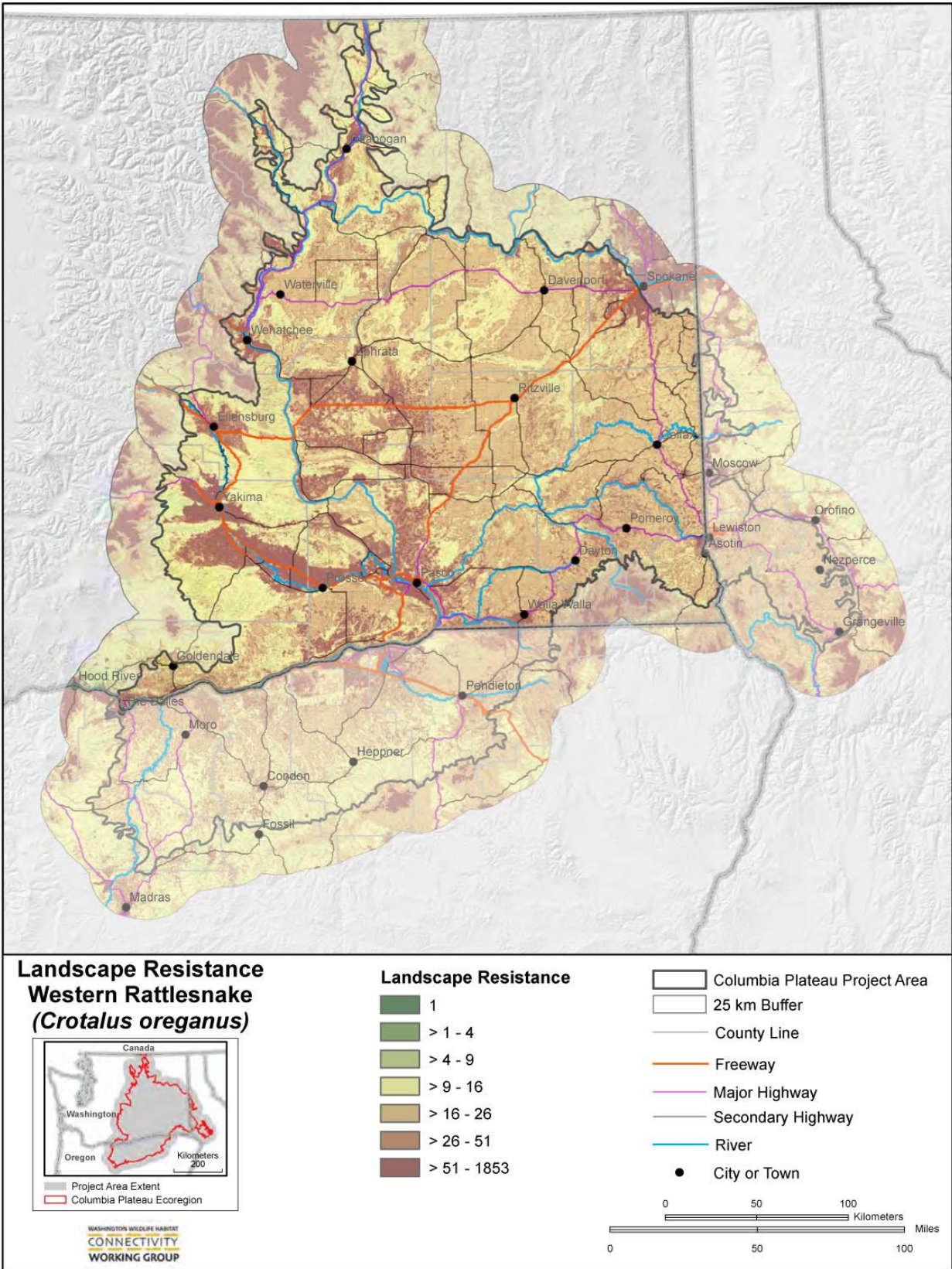


Figure A.9.3. Resistance map for Western rattlesnakes in the Columbia Plateau Ecoregion.

Habitat Modeling and Habitat Concentration Areas

The Maxent habitat model led to 106 different habitat concentration areas (HCAs) across the Columbia Plateau Ecoregion and buffer (Fig. A.9.4). Interestingly, the HCA extent is much reduced compared to the GAP distribution predictions (Cassidy et al. 1997). In particular, the counties of Spokane, Adams, Whitman, and Franklin have extensive predicted GAP habitat, but very little HCA habitat. This is partially due to the fact that HCAs are meant to model ideal habitat and not every area occupied by the species. However, it is also likely that much of the GAP distribution was historically good rattlesnake habitat, but now is no longer suitable due to agriculture or urban modifications. As the habitat map (Fig. A.9.1) suggests, HCAs are concentrated along riverine corridors and are quite linear. The riverine corridors are primarily the Columbia River, the Snake River, and the Okanogan River. HCAs that do not occur along riverine corridors are generally small patches.

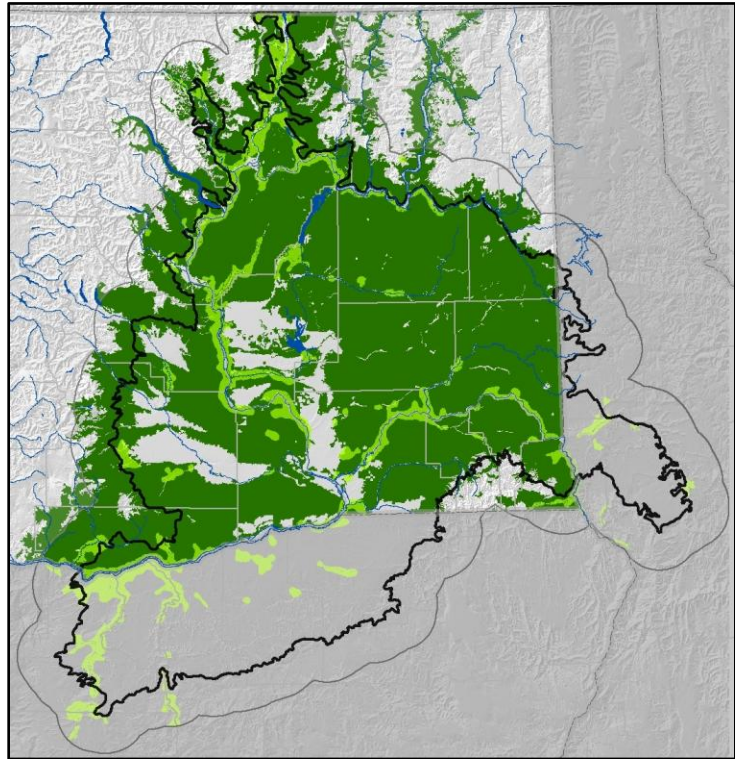


Figure A.9.4. Western rattlesnake HCAs (light green) and GAP distribution (dark green) in the Columbia Plateau Ecoregion.

Habitat concentration areas primarily occur in the western and northern part of the Columbia Plateau, with the exception of the Snake River corridor that extends into Idaho.

The average HCA size is 92 km², but this is skewed high because of the large riverine corridor HCAs, as the median value is 36 km². Thus, the pattern of HCAs suggests that rattlesnake populations are concentrated along river canyons but there are a large number of satellite areas that probably have smaller populations. Many of these small satellite areas are located at or near tributaries to the main river systems, highlighting the importance of these areas for rattlesnakes across the Columbia Plateau.

Cost-Weighted Distance Modeling

Cost-weighted distance values increase rapidly across the Columbia Plateau for Western rattlesnakes (Fig. A.9.5; see also Fig. A.9.6 for HCA identification). In fact, two-thirds of HCAs within 50 Euclidean kilometers of each other are separated by greater than 50–100 km of cost-weighted distance. Based on the cost-weighted distances, most connectivity among HCAs appears to follow the river corridors and it is much more difficult to maintain connectivity across river systems. Exceptions include connections between the Hanford Site and the Lower Crab Creek (HCAs 46, 49, 61, 62, and 64), which are only separated by a road. Across the Yakama Reservation, HCAs 68, 70, and 73 are connected by 50–100 km of CWD. Along the border of

Whitman and Adams counties, there are lower CWD connections between HCAs 3, 45, and 67. Not surprisingly, these are the areas highlighted in the resistance modeling section as areas of low resistance. Overall, I penalized features such as roads and agriculture with high resistances, and this explains why CWD increases rapidly unless HCAs are nearby.

Linkage Modeling

There were 226 linkages that fit within the criteria of a Euclidean distance of 50 km or less, and all HCAs were connected to at least one other (Fig. A.9.7; see also Fig. A.9.6 for HCA identification and Appendix B for full linkage statistics). On average each HCA had four connections. The number of intact linkages is reduced to 201 if we restrict linkages to those with a non-weighted least-cost path distance of 50 km or less, and only 49 had a cost-weighted distance less than 50 km. Thus, while the landscape is well-connected for rattlesnakes based on Euclidean distance, the estimated landscape resistance suggests connectivity has been dramatically altered by anthropogenic development. In fact, relying on a CWD cutoff of 50 km would mean only 62 HCAs had at least one connection, so 44 HCAs are isolated at this threshold. It is difficult to assess whether a cutoff of 50 km CWD is truly meaningful since the resistance values are not empirically determined, but it is likely that at least some formerly connected populations are now isolated.

For the linkages shown in Figure A.9.7, the average Euclidean distance was 15 km, but the standard deviation was almost equal to the mean with a value of 14.6. The average CWD was 281, with a similarly high standard deviation (271). This leads to a high ratio of CWD to Euclidean distance of 29, with a large range of 9–375. However, the distribution is right-skewed and the median value 19, so very few linkages have extremely high ratios.

Habitat concentration area (HCA) 52 has 11 linkages connected to it, the most of any HCA. This HCA is the third largest HCA, and spans the western side of the Columbia River from Wenatchee south through the Yakima Training Center. However, the quality of these linkages are not better than average, as the mean ratio of CWD to Euclidean distance is 28. However, this HCA clearly represents a core area for rattlesnake connectivity and thus of conservation merit. The next most linked HCAs have eight linkage connections, and there are five HCAs (15, 17, 34, 57, and 64) that have this number of linkages. These five HCAs occur in three different regions of the Columbia Plateau. HCAs 15, 17, and 34 are south of Okanogan, and include the west side of the junction of the Okanogan River and the Columbia River, the east side of the Columbia River from the Okanogan junction south to Wenatchee, and the area north of the Columbia River in the vicinity of Omak Lake. HCA 57 is on the north side of the Snake River in Whitman County. Finally, HCA 64 is in the Lower Crab Creek area. However, two of the HCAs (15 and 34) in the Okanogan complex have very high mean CWD to Euclidean distance ratios (47 and 57) so actual connectivity from these HCAs may be lower than expected based on number of linkages. The other three HCAs have CWD to Euclidean distance ratios around the average overall value. Taken together these highly connected rattlesnake HCAs suggest a primary pattern of connectivity linking the Okanogan Valley through the Columbia River to the Snake River into Idaho.

It might also be instructive to examine the paths that have the lowest CWD to Euclidean distance ratio, and thus the least-resistant linkages for rattlesnake movement. The five lowest ratios are the following HCA linkages: 36–41, 103–104, 68–73, 73–94, and 9–15. These linkages

correspond to the Moses Coulee area near Wenatchee, the northwest corner of the study area in Oregon, the Yakama Reservation (two linkages), and near the British Columbia border. While the two northern linkages are part of or near the highly connected HCAs described in the previous paragraph, this analysis identifies Yakama Reservation as a key area for connectivity that is largely separate from the highly connected HCAs. In fact, it appears that populations on the Yakama Reservation are best connected to the Columbia River Gorge on the Washington-Oregon border.

On the other hand, there are four HCAs (2, 5, 86, and 106) that are connected only to one other. Habitat concentration area 2 is along Upper Crab Creek in southern Lincoln County, HCA 5 is around the Methow Valley, HCA 86 is Hells Canyon on the Idaho/Oregon border, and HCA 106 is near Madras, Oregon. However, with the exception of HCA 106, the CWD to Euclidean distance ratios of these single linkages are below average, and thus these HCAs may still be connected because of low resistance. However, it does identify the Methow Valley, Hells Canyon, and Upper Crab Creek as areas where low resistance should be maintained to avoid isolating populations.

(continued on page A.9-23)

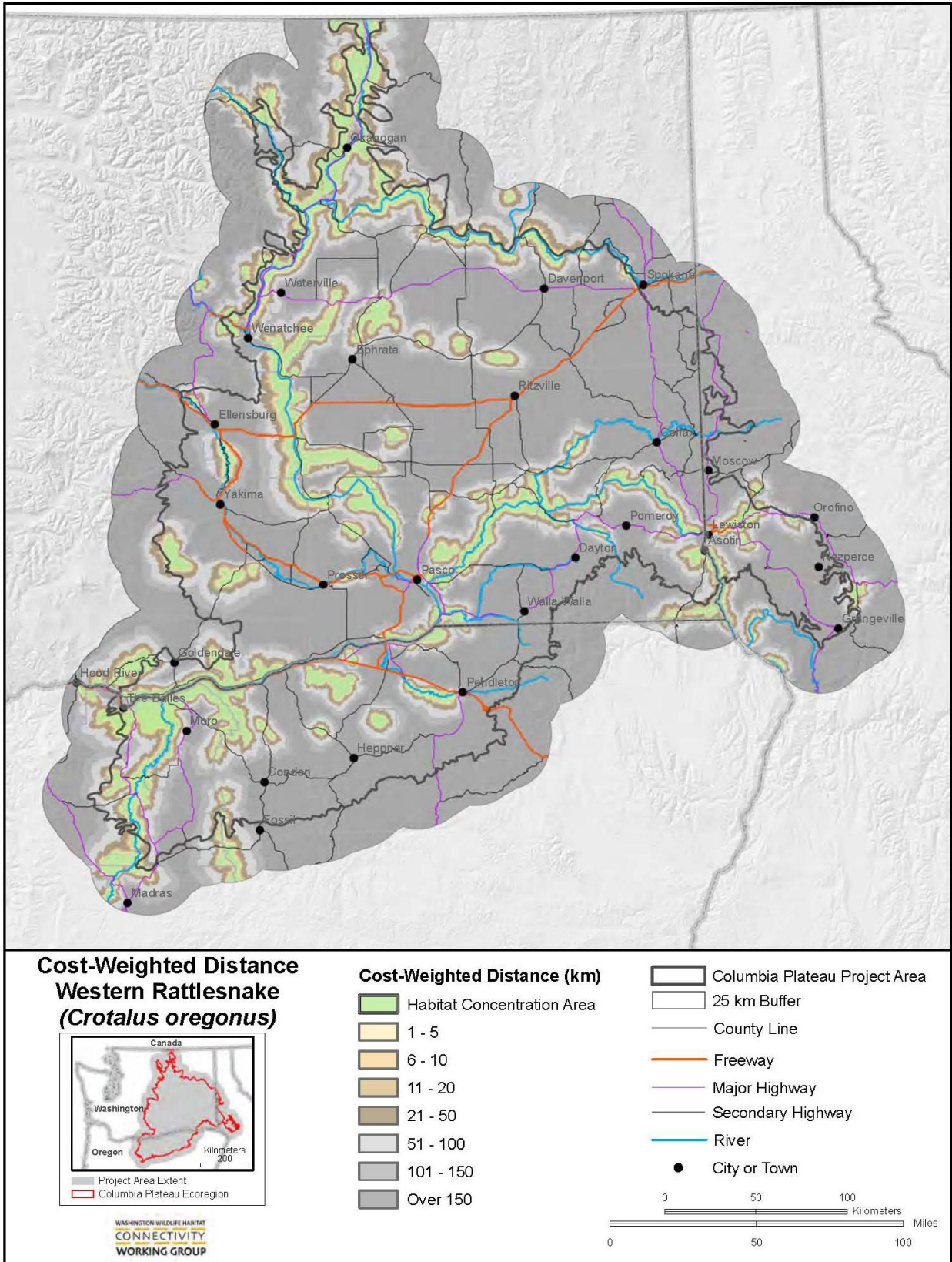


Figure A.9.5. Cost-weighted distance map for Western rattlesnakes in the Columbia Plateau Ecoregion.

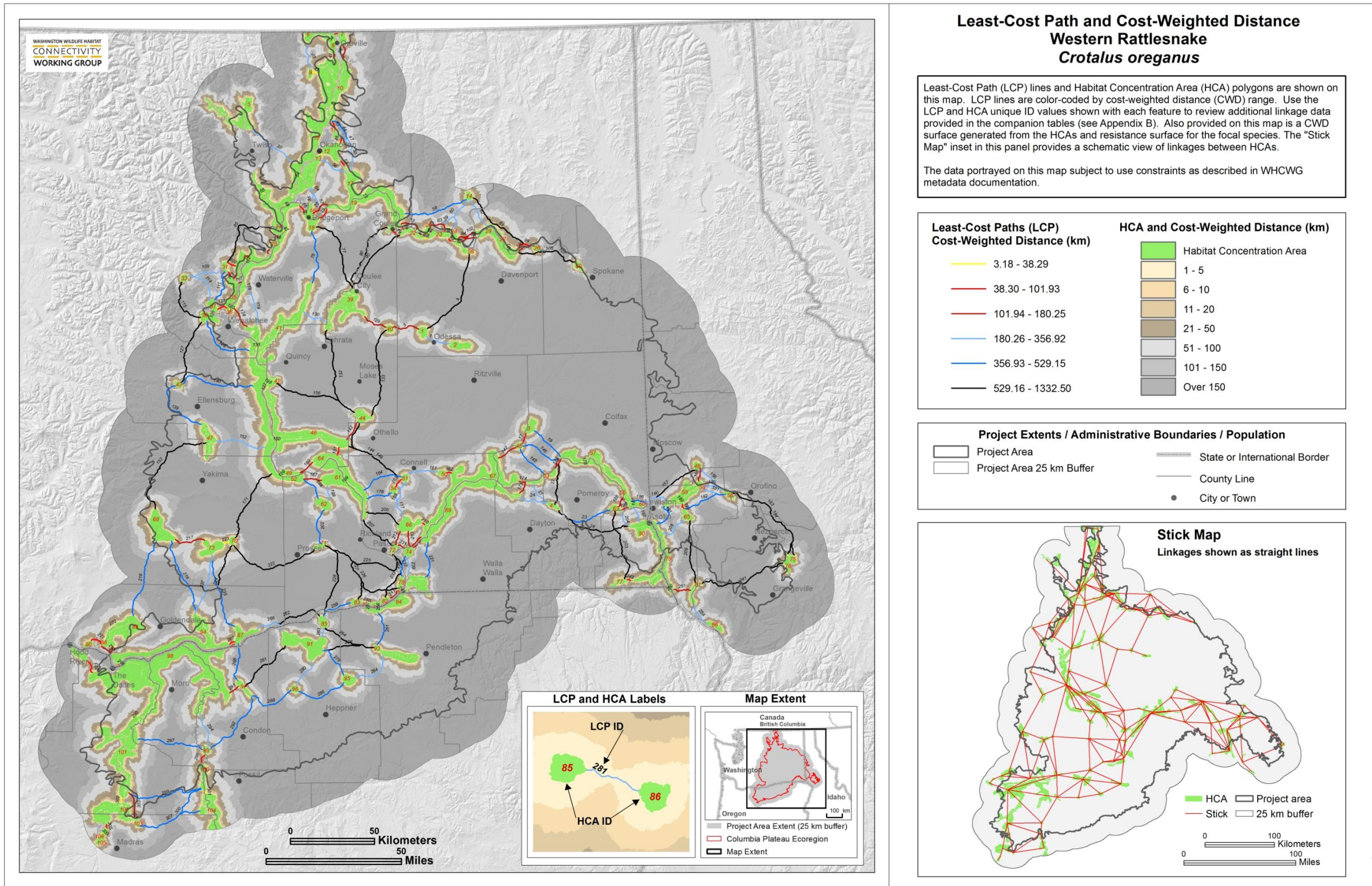


Figure A.9.6. Cost-weighted distance map with numbered HCAs (green polygons labeled with red numerals) and least-cost paths (lines labeled with black numerals) for Western rattlesnakes. Linkage modeling statistics provided in Appendix B.

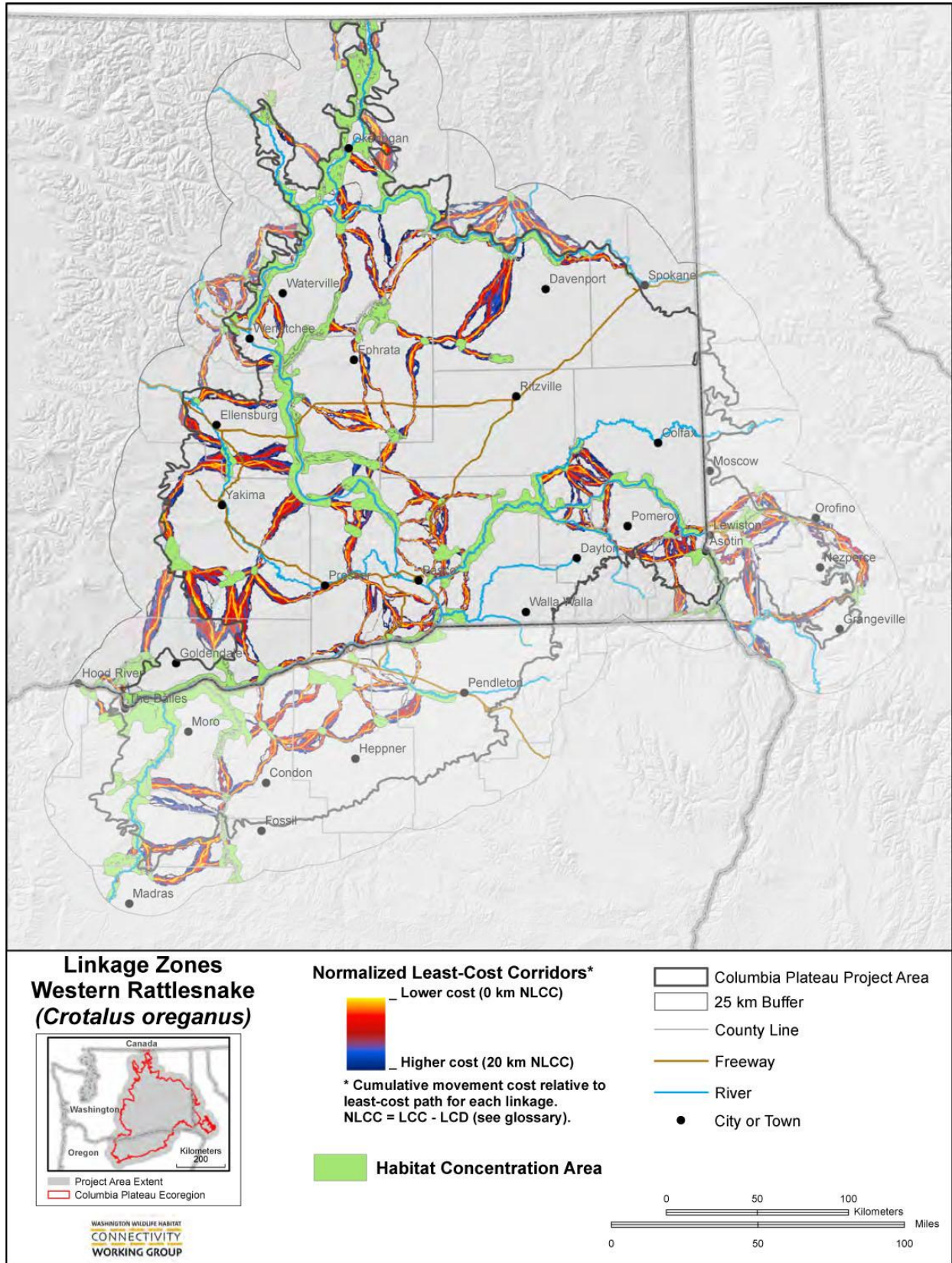


Figure A.9.7. Linkage map for Western rattlesnakes in the Columbia Plateau Ecoregion.

Key Patterns and Insights

Key patterns and insights for our connectivity analysis of Western rattlesnakes in the Columbia Plateau Ecoregion include:

- Roads, housing, high elevations and agriculture are projected to be most resistant to rattlesnakes.
- As a result, low resistance landscapes for Western rattlesnakes are concentrated primarily in restricted or low-use areas.
- HCAs are mostly located along river corridors and are long and linear, and are missing from areas where agriculture is predominant.
- Assuming a 50 km linear dispersal ability all HCAs have at least one connection, with an average of 4 per HCA.
- Overall, there is a high CWD to distance ratio indicating many linkages have high resistance.
- The main connectivity corridor for rattlesnakes is the Columbia River running north-south and the Snake River running east-west.
- There is a smaller connectivity corridor running from the Yakama Reservation to the Columbia River Gorge into Oregon.
- Upper Crab Creek in Lincoln County, Hells Canyon, and the Methow Wildlife Area are regions of current predicted connectivity but are only connected by a single linkage.

Considerations for Future Modeling

There are a number of aspects that could improve the modeling effort. First, it would be advantageous to have observation data that was categorized into den, migration, and foraging habitat. This would allow us to develop habitat models for each separate type of habitat use, which could then be later combined to give a more accurate HCA of total habitat use. Additionally, the habitat modeling effort could benefit from additional rattlesnake surveys across restricted-access lands, particularly the Yakima Training Center and Yakama Reservation. Both these areas are apparently important for connectivity, but we have very few observations in these areas to confirm this.

There are some additional variables that, if included, could possibly improve the model. Rattlesnakes are sensitive to climatic variables, and so inclusion of climate could improve the habitat and resistance models. It would also be valuable to have more information about the influence of infrastructure from wind energy development on reptile populations. I suspect that the roads leading to wind turbines would be highly resistant to rattlesnakes, but there is as yet no data to test this hypothesis. Another additional possibility would be to consider biotic variables in habitat or resistance modeling. Incorporating biotic variables would be difficult, but rattlesnake summer habitat is highly dependent on food sources, and high-quality prey habitat might be very important for predicting rattlesnake habitat use (Jenkins & Peterson 2008). For instance, ground squirrels are an important prey source for Western rattlesnakes; 80% of prey

biomass of rattlesnakes in southwestern Idaho was ground squirrels (Diller & Wallace 1996). As two species of ground squirrels are included in the Columbia Plateau modeling effort, we could use the HCA and connectivity data from the ground squirrels to refine the rattlesnake models.

Further investigation into the sensitivity of particular resistance parameter values would also be useful. For instance, if altering the assigned resistance value of roads or agriculture significantly changed linkage corridors then there would be greater uncertainty in the predicted surface than if changing exact parameter values did not substantially change the final result. Furthermore, it would be useful to estimate resistance surfaces for known radio-telemetry studies of rattlesnakes outside the study area that would help set the cost-weighted distance (CWD) thresholds. Currently, we know rattlesnakes can move a total of 40–50 km in Alberta (Jørgensen et al. 2008), but have no information on the resistance of that landscape to translate into CWD units.

Opportunities for Model Validation

The regional scale of this analysis lends itself very well to a genetic study to validate the connectivity models. While movement studies such as radio-telemetry can be insightful for connectivity studies, the broad extent of this effort prevents methods such as radio-telemetry being effectively used across the entire area. However, tissue samples could be collected using a subsample of the HCAs, and the genetic distance among HCA populations could then be correlated with the resistance surface. Furthermore, the genetic data could be used to optimize parameter values on the resistance surface. Another advantage of genetic data is that it only represents movement that has led to successful reproduction, and as a result, provides a measure of functional connectivity for the long-term viability of the populations. Additional survey data would also be useful to validate HCAs that occur in locations that are less sampled for rattlesnakes.

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Literature Cited

- Andrews, K. M., J. W. Gibbons, and D. M. Jochimsen. 2008. Ecological effects of roads on amphibians and reptiles: A literature review. Pages 121–143 in J. C. Mitchell, R. E. Jung Brown, and B. Bartholomew, editors. *Urban Herpetology, Herpetological Conservation #3*, Society for the Study of Amphibians and Reptiles, Salt Lake City.
- Bauder, J. M. 2010. Movements and habitat selection of prairie rattlesnakes (*Crotalus v. viridis*) across a mountainous landscape in a designated wilderness area. Master's thesis. Idaho State University, Pocatello, Idaho.

- Cassidy, K. M., C. E. Grue, M. R. Smith, and K. M. Dvornich, editors. 1997. Washington State Gap Analysis-Final Report. Volumes 1-5. Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Seattle.
- Clark, R. W., W. S. Brown, R. Stechert, and K. R. Zamudio. 2008. Integrating individual behavior and landscape genetics: the population structure of timber rattlesnake hibernacula. *Molecular Ecology* 2008:719–730.
- Clark, R. W., W. S. Brown, R. Stechert, and K. R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in Timber Rattlesnakes. *Conservation Biology* 24:1059–1069.
- Cooper-Doering, S. 2005. Modeling rattlesnake hibernacula on the Idaho National Laboratory, Idaho. Master's thesis. Idaho State University, Pocatello, Idaho.
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2004. Status report on the Western Rattlesnake (*Crotalus oreganus*) in Canada. Prepared for the Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario.
- Didiuk, A. B. 1999. Reptile and amphibian component report; Canadian Forces Base Suffield National Wildlife Area, Wildlife Inventory. Unpublished report by the Canadian Wildlife Service, Environment Canada, Prairie and Northern Region, Edmonton, Alberta, Canada.
- Diller, L. V., and R. L. Wallace. 1996. Comparative ecology of two snake species (*Crotalus viridis* and *Pituophis melanoleucus*) in southwestern Idaho. *Herpetologica* 52:343–360.
- Diller, L. V., and R. L. Wallace. 2002. Growth, reproduction, and survival in a population of *Crotalus viridis oreganus* in north central Idaho. *Herpetological Monographs* 16:26–45.
- Duvall, D., M. B. King, and K. J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. *National Geographic Research* 1:80–111.
- Elith, J., C. H. Graham, R. P. Anderson, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Ernst, C. H., and E. M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Books, Washington DC.
- Fitch, H. S. 1949. Study of snake populations in central California. *American Midland Naturalist* 41:513–579.
- Gienger, C. M., and D. D. Beck. 2011. Northern Pacific rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. *Canadian Journal of Zoology* 89:1084–1090.
- Gomez, L. M. 2007. Habitat use and movement patterns of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in British Columbia. Master's thesis. University of Victoria, Victoria, British Columbia.

- Hamilton, B. T., and E. M. Nowak. 2009. Relationships between insolation and rattlesnake hibernacula. *Western North American Naturalist* 69:319–328.
- Jenkins, C. L. 2007. Ecology and conservation of rattlesnakes in sagebrush steppe ecosystems: Landscape disturbance, small mammal communities, and Great Basin rattlesnake reproduction. PhD dissertation. Idaho State University, Pocatello, Idaho.
- Jenkins, C. L., and C. R. Peterson. 2008. A trophic-based approach to the conservation biology of rattlesnakes: Linking landscape disturbances to rattlesnake populations. Pages 265–274 in W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush, editors. *The Biology of Rattlesnakes*, Loma Linda University Press, Loma Linda, California.
- Jenkins, C. L., C. R. Peterson, S. C. Doering, and V. A. Cobb. 2009. Microgeographic variation in reproductive characteristics among Western rattlesnake (*Crotalus oreganus*) populations. *Copeia* 2009:774–780.
- Jochimsen, D. M. 2006. Ecological effects of roads on herpetofauna: a literature review and empirical study examining seasonal and landscape influences on snake road mortality in eastern Idaho. Master's thesis. Idaho State University, Pocatello, Idaho.
- Jochimsen, D. M., C. R. Peterson, K. M. Andrews, and J. W. Gibbons. 2004. A literature review of the effects of roads on amphibians and reptiles and the measures used to mitigate those effects. Unpublished report, Idaho Fish and Game Department and the USDA Forest Service, Boise, Idaho.
- Jørgensen, D., C. C. Gates, and D. P. Whiteside. 2008. Movements, migrations, and mechanisms: A review of radiotelemetry studies of Prairie (*Crotalus v. viridis*) and Western (*Crotalus oreganus*) rattlesnakes. Pages 303–316 in W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush, editors. *The Biology of Rattlesnakes*, Loma Linda University Press, Loma Linda, California.
- King, M., and D. Duvall. 1990. Prairie rattlesnake seasonal migrations: Episodes of movement, vernal foraging and sex differences. *Animal Behavior* 39:924–935.
- Klauber, L. M. 1939. Studies of reptile life in the arid Southwest. *Bulletin of the Zoological Society of San Diego* 14:1–100.
- Lobo, J. M., A. Jimenez-Valverde, and J. Hortal. 2010. The uncertain nature of absences and their importance in species distribution modeling. *Ecography* 33:103–114.
- NatureServe. 2011. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, VA.
Available from <http://www.natureserve.org/explorer> (accessed 2011).
- Parker, J. M. 2003. The ecology and behavior of the midget faded rattlesnake in Wyoming. PhD dissertation, University of Wyoming, Laramie, Wyoming.

- Parker, J. M., and S. H. Anderson. 2007. Ecology and behavior of the midget faded rattlesnake (*Crotalus oreganus concolor*) in Wyoming. *Journal of Herpetology* 41:41–51.
- Parker, W. S., and W. S. Brown. 1973. Species composition and population changes in two complexes of snake hibernacula in northern Utah. *Herpetologica* 30:234–239.
- Parsons, S. B. 2009. Landscape genetics of Great Basin rattlesnakes, *Crotalus oreganus lutosus*, on the Idaho National Laboratory. Master's Thesis, Idaho State University, Pocatello, Idaho.
- Reed, R. N., and M. E. Douglas. 2002. Ecology of the Grand Canyon rattlesnake (*Crotalus viridis abyssus*) in the Little Colorado River Canyon, Arizona. *The Southwestern Naturalist* 47:30–39.
- Spear, S. F., J. M. Parker, C. R. Peterson, and C. L. Jenkins. 2011. Conservation and management of midget faded rattlesnakes. State Wildlife Grant Final Report to Wyoming Game and Fish Department.
- Sullivan, B. K. 2000. Long-term shifts in snake populations: a California site revisited. *Biological Conservation* 94:321–325.
- VanDerWal, J., L. P. Shoo, C. Graham, and S. E. Williams. 2009. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? *Ecological Modeling* 220:589–594.
- WHCWG (Washington Wildlife Habitat Connectivity Working Group). 2010. Washington Connected Landscapes Project: Statewide Analysis. Washington Departments of Fish and Wildlife, and Transportation, Olympia, Washington.

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